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FEEDING IN THE ARCHAEOCETE WHALE *ZYGORHIZA KOCHII* (CETACEA: ARCHAEOCETI)

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ABSTRACT

In order to test the various feeding hypotheses presented for the archaeocete whale, *Zygorhiza kochii*, the masticatory musculature was restored. This restoration indicates that the important muscle groups in descending order were Temporalis Group - Masseter Group - Pterygoideus Group. This musculature system is typical of carnivores. Tooth wear, in conjunction with the restored musculature, suggests *Zygorhiza* primarily fed on fish, and possibly on squids as well.

INTRODUCTION

Archaeocete whales were the dominant predatory marine mammals of the Eocene (Barnes, Domning, and Ray, 1985). Skeletal remains are distributed globally, indicating just how successful these animals were. Their fossil remains are especially abundant in upper Eocene sediments and have provided a great deal of information about their systematics, anatomy, and functional morphology (e.g. Stromer, 1903, 1908; Kellogg, 1928, 1936; Breathnach, 1955; Edinger, 1955; Fleisher, 1976).

Figure 1. Skull of *Lophodon carcinophagus,* AMNH 2194.

The diet of archaeocete whales is frequently assumed to be fish (e.g. Barnes and Mitchell, 1978), although no detailed morphological evidence has ever been presented in support of this hypothesis. Kellogg (1928) suggested that the long rostrum was used as forceps to catch prey. He also noted that the cheek teeth were serrated, but said nothing about the functional significance of this. Van Valen (1968), in a novel approach, drew attention to the similarities between the serrated cheek teeth of archaeocete whales and of krill-feeding seals, especially *Lophodon* (compare Figures 1 and 2A with Figures 3A and 4B). He, therefore, suggested that archaeocete whales were not fish-eaters, but krill-eaters. This is not an unreasonable hypothesis, as today krill supports the largest endothermic animal of all time, the blue whale.

But is Van Valen correct in his analogy between the teeth of an archaeocete whale and krill-eating seals, or are the similarities of the teeth coincidental? To answer this, and to determine the probable diet of archaeocete whales, we undertook a study of an uncrushed skull and mandible of a specimen of *Zygorhiza kochii* in the collection of the Mississippi Museum of Natural Science. The skull and lower jaws belong to a partial skeleton collected from the Moodys Branch Formation on Thompson Creek, Yazoo County, Mississippi. The discovery of this specimen is presented in Dockery (1974), Frazier (1980), and Carpenter and Dockery (1985). The local geology is also presented in Dockery (1974), and a photographic record of the mounting of the skeleton is given in Carpenter and Dockery (1985).

METHODS

In order to determine the diet and probable method of feeding in *Zygorhiza,* it is necessary to first reconstruct the masticatory musculature. This information will reveal which of the muscles are most important in feeding, and by comparison with the masticatory musculature in extant mammals will allow predictions to be made about feeding strategies and diet. This form of dietary interpretation by reconstruction of jaw musculature has been successfully used in studies of other extinct animals (e.g. Adams, 1919; Szalay, 1969; Turnbull, 1970, 1976; Bramble, 1978).

Reconstruction of the masticatory musculature of *Zygorhiza* was accomplished by locating and identifying the origin and insertion scars on the skull and mandibles. Where the skull or mandibles are damaged or reconstructed, origin and insertion was determined from the figures and plates in Kellogg

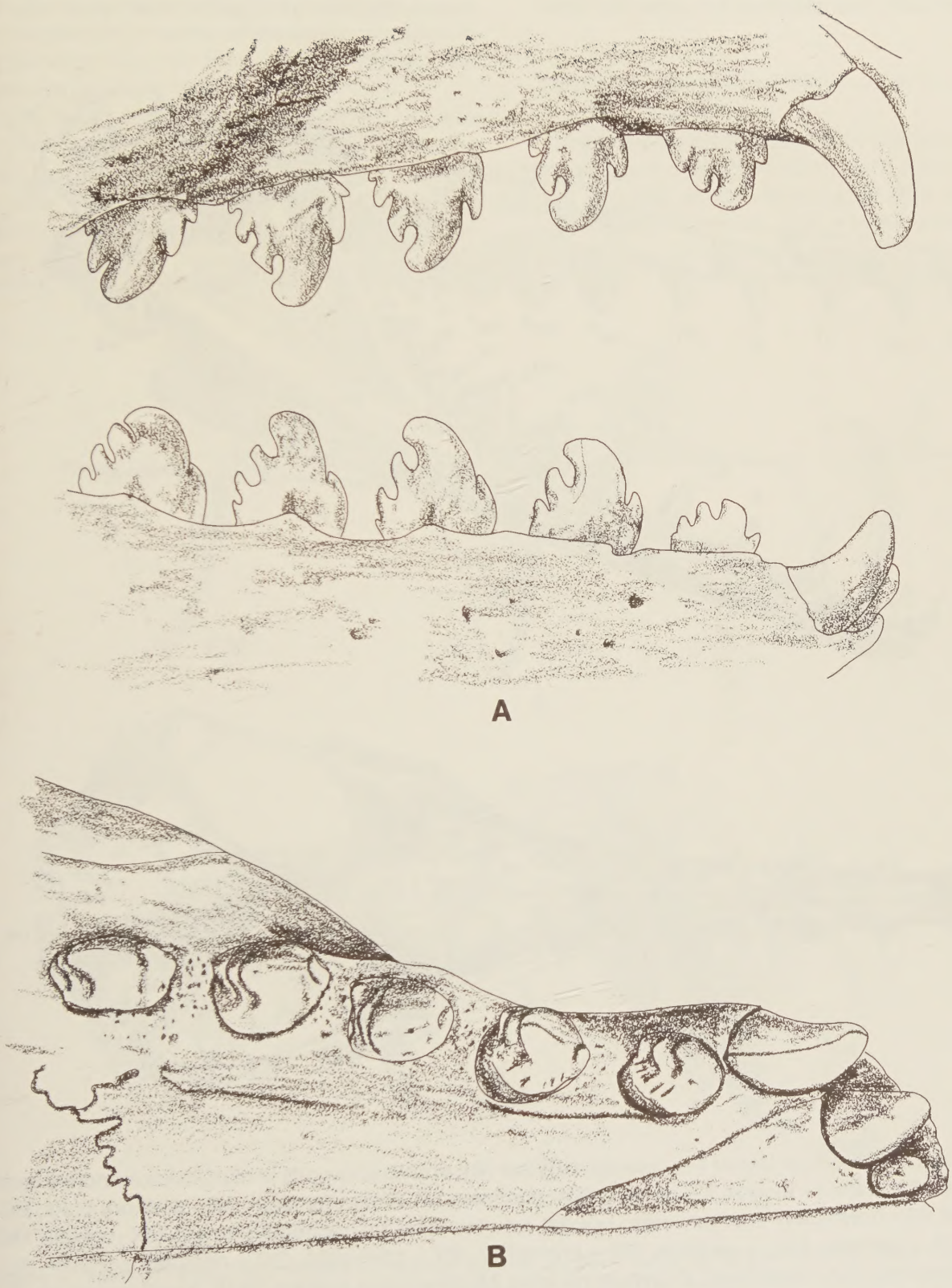

Figure 2. Detail of the teeth of *Lophodon carcinophagus* in lateral (A) and occlusal (B) views; AMNH 2194.

(1936). Identification of the muscles, which made the scars, was determined by comparison with the origins and insertions described for extant mammals (e.g. Turnbull, 1970), and by dissection of a domestic cat obtained from a biological supply house. Studies of extant whales were also used

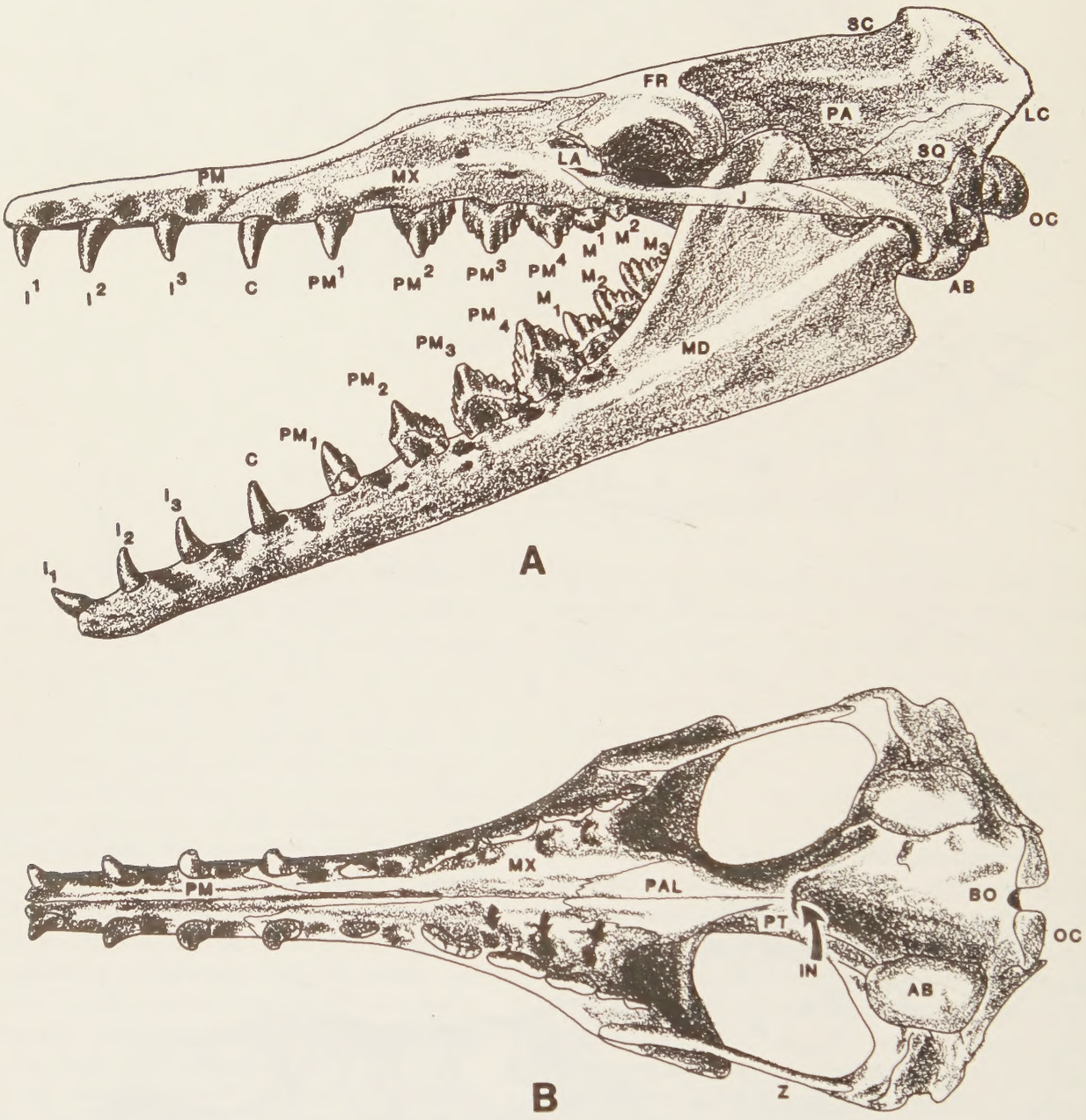

Figure 3. *Zygorhiza kochii* in lateral (A), and ventral view (B); arrows show pits in maxilla for mandible teeth. Abbreviations for teeth: I - incisor, C - canine, PM - premolar, M - molar; for skull: AB - auditory bulla, BO - basioccipital, FR - frontal, IN - internal nares, J - jugal, LA - lacrymal, LC - lambdoidal crest, MX - maxilla, MD - mandible, PA - parietal, PAL - palatine, PM - premaxilla, PT - pterygoid, OC - occipital condyle, SC - supraoccipital crest, SQ - squamosal, Z - zygomatic arch. Modified from Kellogg, 1936. A well preserved skull on display at the Mississippi Museum of Natural Science has a more evenly tapered snout than the one illustrated here.

Schultze and Smith, 1918; Howell, 1927), but these have limitations due to the structural modifications of the modern whale skull. The muscle data were then transferred to figures of the skull and mandible of *Zygorhiza* adapted from Kellogg (1936). The results are shown in Figures 5 - 8.

Tooth wear in dietary interpretations is also important, because it is resistance of the food during eating that causes wear (Kraus, 1982). Therefore, the wear of teeth in the skull and mandible of *Zygorhiza* was examined with a binocular microscope. In addition, detached teeth of *Zygorhiza kochii* (U.S. National Museum 11962) were also examined in order to determine if there was any abnormal wear of the teeth in the skull and mandibles used in our study.

DESCRIPTION OF THE SKULL AND MANDIBLE

Kellogg (1936) presents a detailed description of the skull and mandible of *Zygorhiza kochii,* and the new material of our study adds little additional information. Therefore, only a brief description of the skull and mandible of *Zygorhiza* is presented here.

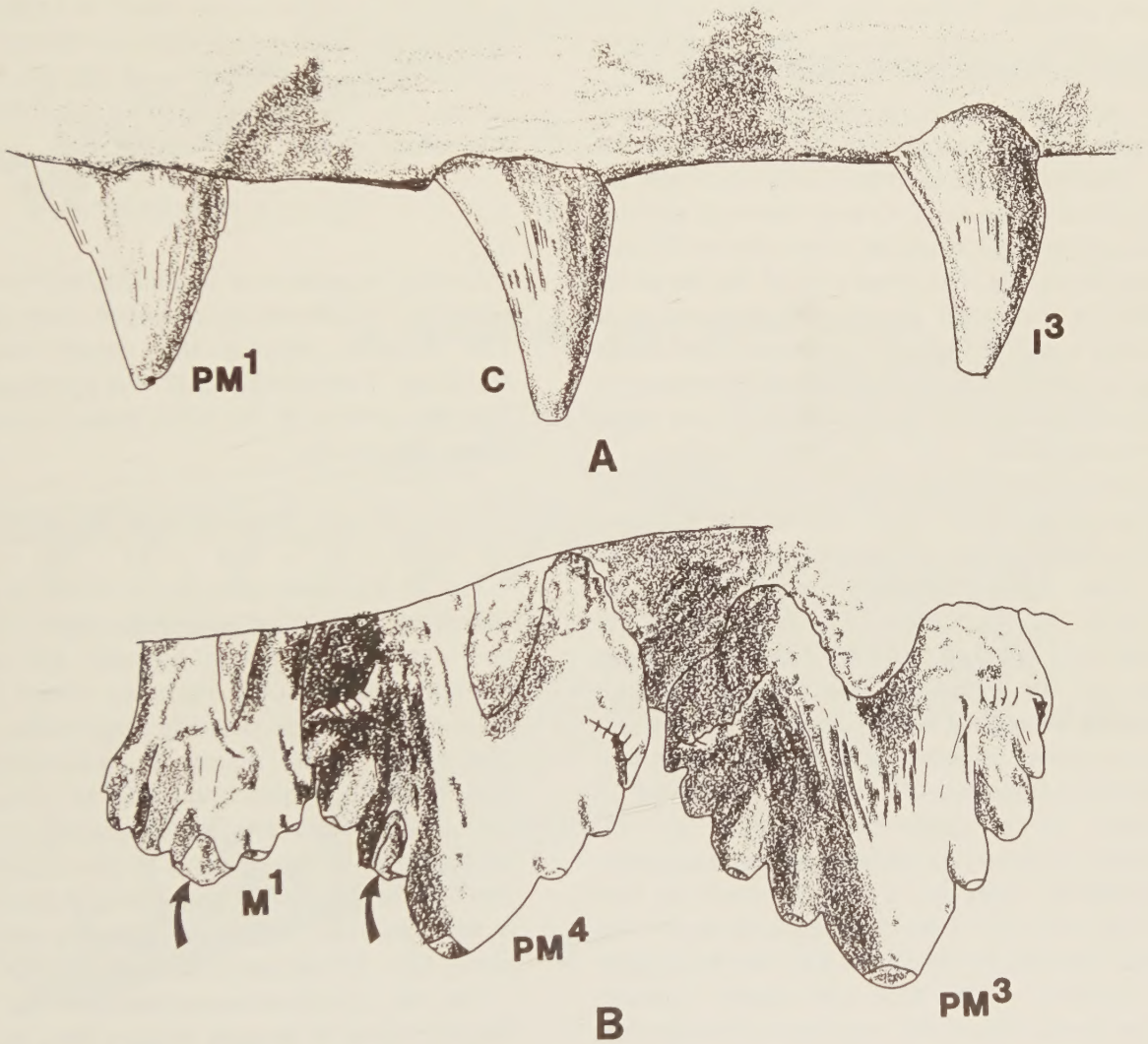

Figure 4. Teeth of *Zygorhiza kochii.* A, buccal view of anterior teeth. B, lingual view of cheek teeth; arrows show chipping of enamel. Abbreviations: C - canine, I - incisor, M - molar, PM - premolar. Modified from Kellogg, 1936.

The skull used in this study (see Dockery, 1974, Figure 1), measures 830 mm from the tip of the premaxillary to the occipital condyle. The skull of *Zygorhiza* is typical of an archaeocete. In profile it is long and low, and wedge shaped, with the highest point at the sagital crest and tapering anteriorly to the tip of the snout (Figure 3A). The orbits are small and open posteriorly. The zygomatic arch is slender, but much less so than in extant cetaceans. An elongated rostrum is formed by the elongation of the premaxillaries and anterior portion of the maxillaries. This results in the teeth being widely spaced, thus accommodating the teeth of the mandible when the mouth is closed (Figure 9).

Viewed dorsally (Figure 7B), the skull is wedge shaped, being widest across the postglenoid process of the squamosal. The rostrum is long and may be tapered or nearly parallel-sided. It is sharply demarcated from the cranium just in front of the orbits. The large external nares is situated near the anterior third of the skull. One of the most striking features of the skull in dorsal view is the enormous temporal fenestrae. The large size of the temporal fenestrae is increased by the development of a lambdoidal crest. The enormous temporal fenestrae are many orders of magnitude larger than seen in any extant whales, and clearly indicate very large temporalis muscles.

The ventral view of the skull (Figure 3B) reflects the dorsal view of the skull in overall shape, broad posteriorly and a long tapered snout. The internal nares open more posteriorly than the typical mammalian condition by the medial union of the palatines and pterygoids. This provides a larger surface for the origin of the M. pterygoideus internus. The auditory bullae, large and dense, are similar to those of extant whales. Lateral to the auditory bulla is the mandibular fossa. It is closed off posteriorly by a descending process of the squamosal, the postglenoid process of the squamosal. Anteriorly, however, it remains open so that there is no retention of the mandibular condyle. The dentition can be divided into two morphological types: anterior teeth that are widely spaced, recurved cones (Figure 4A), and posterior teeth that are closely set, triangular, laterally compressed, and have large denticulations on the anterior and posterior edges (Figure 4B). The transition between the widely spaced conical teeth and the closely spaced triangular teeth occurs at the first premolar. It is a laterally compressed conical tooth, but with denticulation along the posterior margin. The space between the anterior teeth is scalloped to accommodate the opposing teeth when the mouth is closed (Figure 4A). When the mouth is closed the lower posterior teeth set into deep pits lingual to the cheek teeth (Figure 3B).

The mandibles are long and slender and have a symphysis almost half their length (Figure 8A, B). The dentition is similar to that of the skull. Unlike extant whales, the coronoid process is very large and well developed, as is the mandibular condyle. No mandibular fossa is present on the lateral surface, a condition also seen in extant whales. There is, however, a low ridge that divides the outer surface of the mandible (Figure 3A). On the medial surface, the mandibular foramen is enormous, as it is in extant whales.

MUSCLE RESTORATIONS

Cranial muscles may be divided into those which close the mouth and those which open the mouth. The muscles closing the mouth include the Masseter, Temporalis and Pterygoideus groups. The digastricus is the only major muscle which opens the mouth.

Masseter Group

The M. masseter pars superficialis is a massive triangular shaped muscle (Figure 5A). It probably had a tendinous origin beneath the orbit. The muscle widened posteriorly to insert along the posterior and posteroventral edge of the mandible. The muscle fibers appear to have been inclined about 30° below horizontal. The M. masseter pars profunda is wedge shaped (Figure 5B). It originates along the outer lower edge of the zygomatic arch and inserts along the ridge dividing the outer surface of the mandible. These muscle fibers were oriented about 45° - 50° below horizontal.

The M. zygomaticomandibularis is a wedge shaped sheet of muscle (Figure 6A). It originates along the lower edge of the zygomatic arch and inserts along the upper edge of the dividing ridge on the outer surface of the mandible. The muscle fibers are about 70° from horizontal.

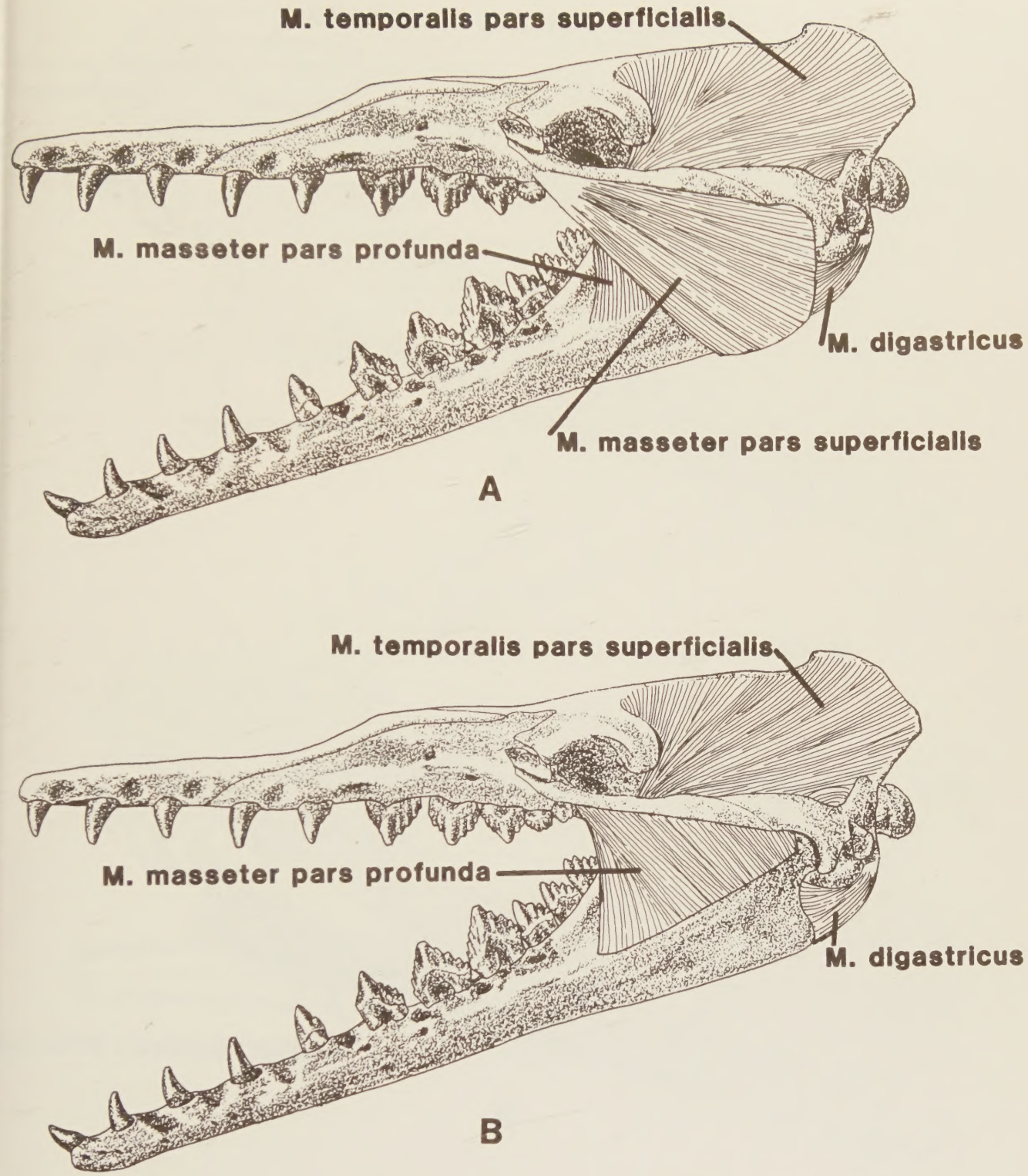

Figure 5. A, superficial muscles. B, after removal of M. masseter pars superficialis.

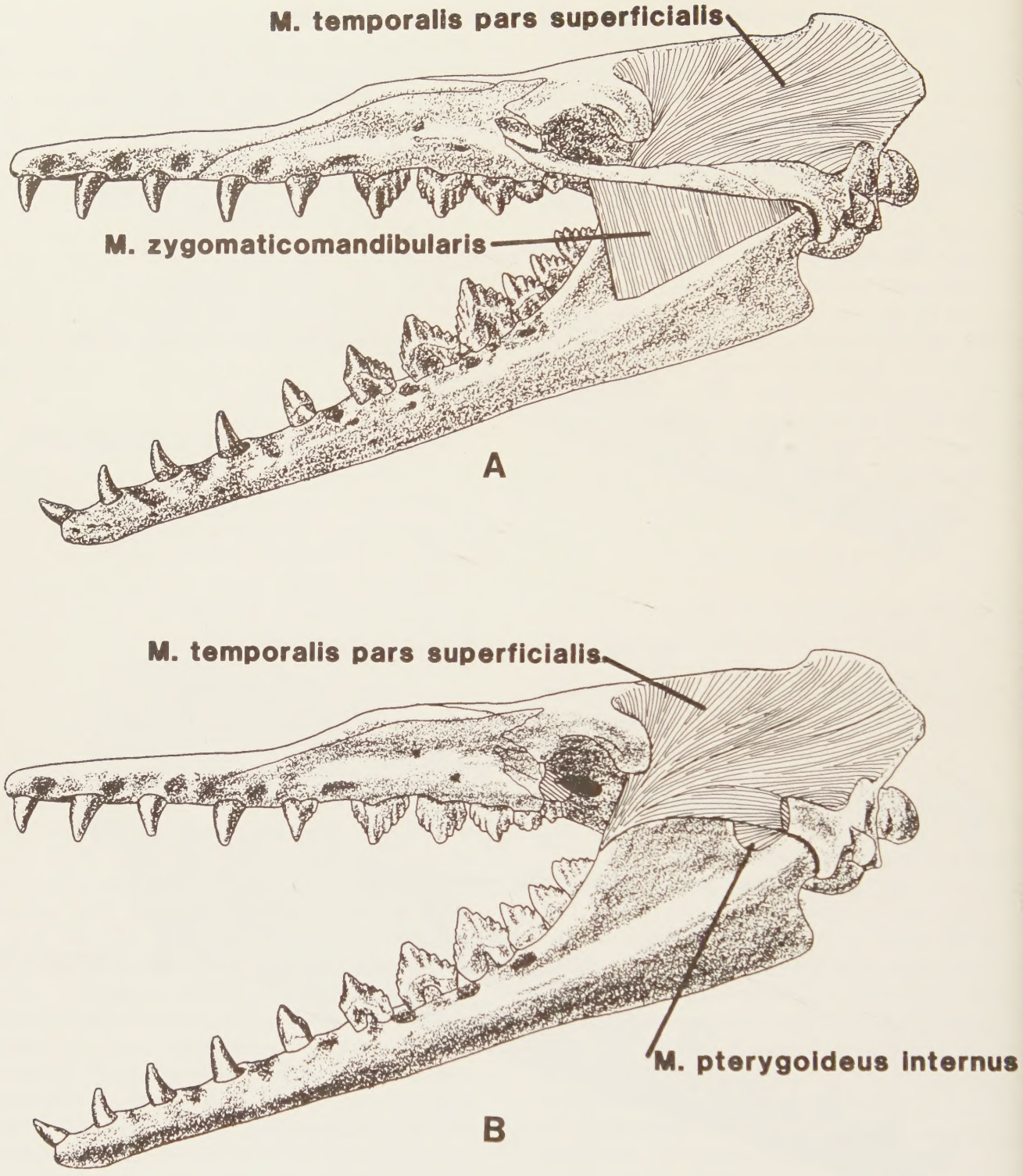

Figure 6. A, after removal of M. masseter pars profunda. B, after removal of M. zygomaticomandibularis.

Temporalis Group

The M. temporalis is massive (Figure 7B), completely filling the temporal fossa. The muscle was separated from the orbit by the postorbital ligament. A heavy aponeurosis covered the muscle and served as the origin of the more superficial parts of the M. temporalis pars superficialis. The deeper

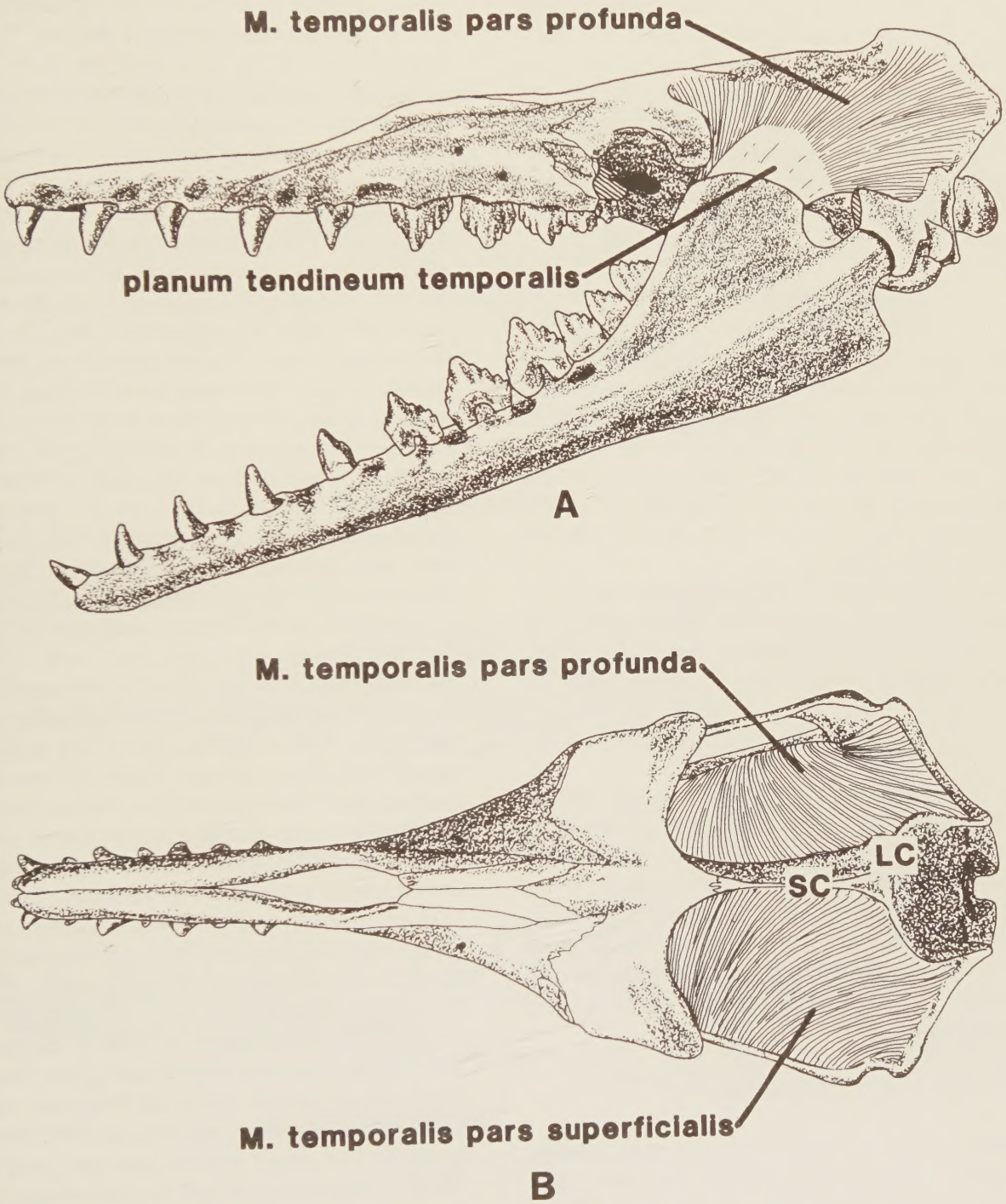

Figure 7. A, after removal of M. temporalis superficialis. B, dorsal view of the Temporalis Group. Abbreviations: LC - lambdoidal crest, SC - supraoccipital crest.

parts of this muscle originate along the sagital and lambdoidal crests (Figures 6B, 7B). The muscle fibers behind the orbit are almost vertical, while those originating from the lambdoidal crest are almost horizontal. All of the fibers converge and insert along the front and outer surface of the coronoid process. The M. temporalis pars profunda underlies the pars superficialis (Figure 7A, B). It originates from the lateral wall of the braincase below the sagital and lambdoidal crests. As with the pars superficialis, the more anterior fibers are vertical, while the more posterior ones are horizontal. The fibers converge and insert on a sheet-like tendon, the planum tendineum temporalis (Figures 7A, 8B).

Pterygoideus Group

The M. pterygoideus internus has two points of origin in extant whales (Howell, 1927). The largest slip originates along the palatine and pterygoid lateral to the internal nares, while the second, smaller slip apparently originates medial to the auditory bulla (Figure 8A). Both slips converge and insert along the lower medial surface of the mandible (Figure 8B).

Dorsal to the M. p. internus is the origin of the M. pterygoideus externus (Figure 8A, B). This is a short, thick muscle with a tendinous insertion on the medial surface of the mandibular condyle.

Digastricus Group

The M. digastricus (Figure 5A, B) is a short, thick muscle with two bellies separated by a tendon. The posterior belly originates on the paroccipital process, crosses over the lateral surface of the auditory bulla and inserts on the dividing tendon, possibly opposite the mandibular angle. The anterior belly has its origin with the dividing tendon and inserts along the lower inner edge of the mandible (Figure 8B).

DISCUSSION

Turnbull (1970) devised a classification scheme for mammal masticatory systems. *Zygorhiza* best fits into his Specialized Group I: long snout; fast, powerful, generalized jaw closing musculature dominated by the Temporalis Group muscles, followed by the Masseter Group muscles, and last the Pterygoideus Group muscles; straight hinge, scissors type jaw movement; and grasping, piercing, and shearing dentition. All of these features characterize adaptations for predation.

The long tapered snout has simple conical teeth which interlock when the mouth is closed (Figure 9). These teeth all show wear at their tips (Figure 4A) from food-to-tooth wear, and not from tooth-to-tooth wear. A long snout with interlocking simple conical teeth is typical for piscivorous vertebrates, such as the gavial or porpoise. The snout is well suited for grasping prey, and the well developed Temporalis Group muscles insure that the mouth closes rapidly before the prey can escape.

The cheek teeth show wear of the denticulation tips (Figures 4B, 11), which also indicates food-to-tooth wear. Although the cheek teeth are laterally compressed, none of them ever shows wear facets caused by the lower teeth shearing past the upper teeth. Instead, some of them show chipping of the enamel. This chipping is on the lingual side of the maxillary teeth (Figure 4B) and suggests either occasional tooth-to-tooth contact, and/or occasional contact with very resistant hard parts in the prey, such as bone. The tooth-to-tooth contact may be the result of the lateral mobility of the mandibles as indicated by the almost hemispherical shape of the mandibular condyle. The long symphysis prevented separate movement of the mandibles, but they may have moved in concert towards one side or the other. Hiimae (1978) noted that typically the lower jaws move straight down as the mouth is opened, then move laterally at the start of the bite, and finally move medially just before or just when there is tooth-to-tooth contact. The jaws, then, move through a "D" pattern. With *Zygorhiza*, the mandible may have moved through a similar pattern, although the jaws moved medially before there was tooth-to-tooth contact (except on rare occasions). This cycle is shown in Figure 12.

We envision that once the prey is caught by the piercing incisors, it is then sliced by the cheek teeth. As the mouth closes, almost all the cheek teeth pass each other simultaneously (Figure 10B). This occurs because the upper molars become progressively smaller posteriorly so that the last molars pass one another about the same time as the second premolars. The triangular shape of the cheek teeth catches the prey between the teeth, preventing

escape (Figure 10A). Because of the apparent absence of shear between opposing teeth, as occurs with the carnassials of cats, it is most likely that the dominant prey was large fish rather than mammalian (i.e. another whale). This is because muscles of mammals are bundles of long fibers that must be cut, but the muscles of fish are arranged as myomeres that can be easily separated. By this we do not imply that *Zygorhiza* was exclusively a fish-eater; it was probably opportunistic as most mammalian carnivores are. We certainly do not consider *Zygorhiza* to be the Killer Whale of the Eocene. In fact, we see no

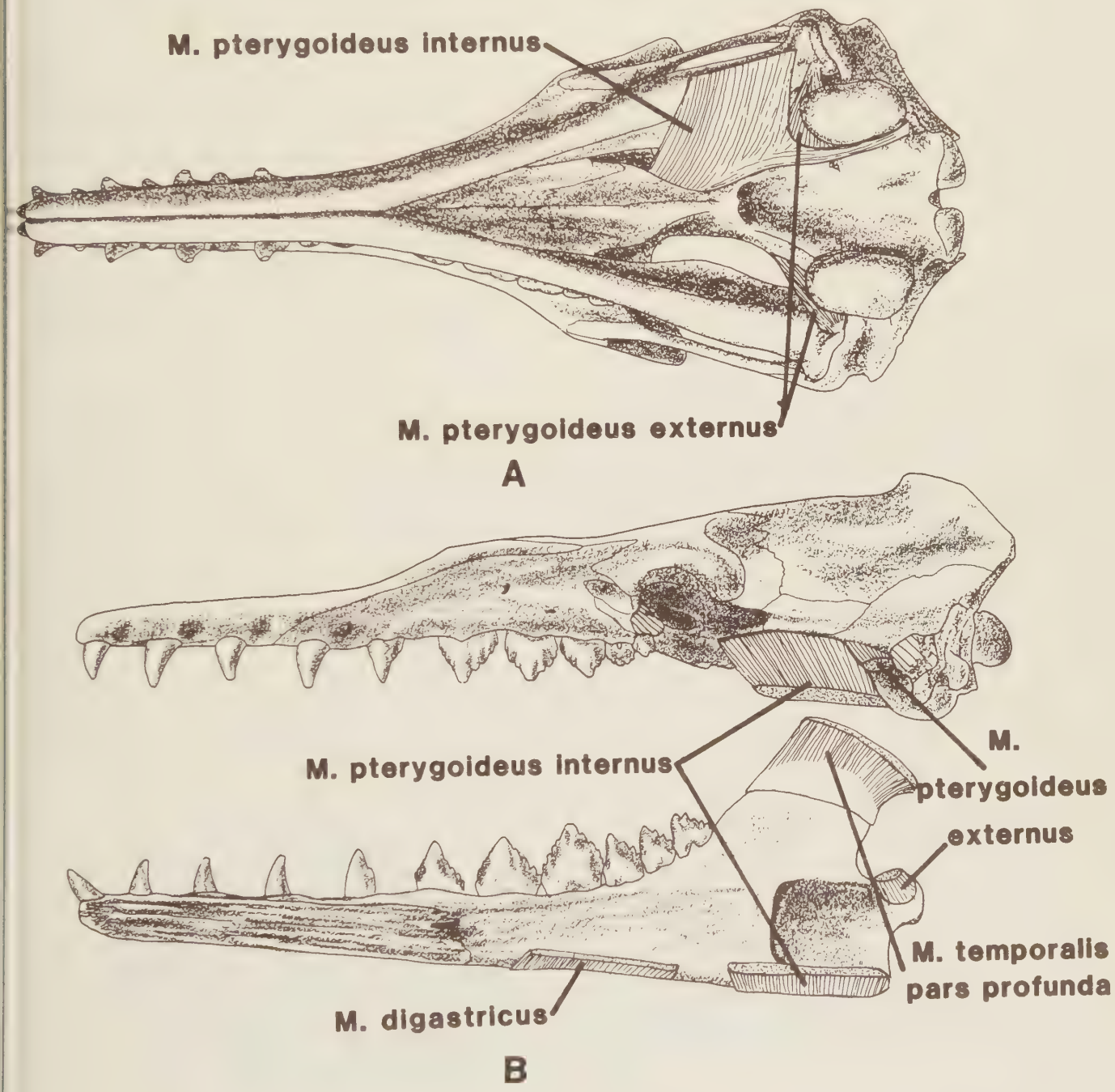

Figure 8. A, ventral view of the Pterygoideus Group. B, origins and insertions for the Pterygoideus Group and the digastricus.

evidence from any of the archaeocetes to indicate that the Killer Whale niche was filled during the Eocene.

As for the hypothesis that *Zygorhiza* was a krill-eater, the similarities between the teeth are more apparent than real. In profile the teeth of the krill-eating seal, *Lophodon carcinophagus,* do show large denticulations similar to those of the cheek teeth of *Zygorhiza* (compare Figures 2A and 4B). However, the teeth of *Zygorhiza* are laterally compressed blades, while those of *Lophodon* are not (compare Figures 2B and 11B). Furthermore, the denticulation of the cheek teeth in *Zygorhiza* shows wear on the tips from food-to-tooth contact, whereas that of *Lophodon* does not (compare Figure 2A, B, with Figures 4B, 11).

CONCLUSIONS

Because of the well developed masticatory musculature, especially the Temporalis Group, we conclude that *Zygorhiza kochii* was a carnivore feeding primarily upon fish. The similarities between the teeth of the krill-feeding seal, *Lophodon carcinophagus,* and those of *Zygorhiza* are more apparent than real, and do not support the hypothesis that *Zygorhiza* or any other archaeocete was a krill-eater.

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Figure 9. *Zygorhiza kochii* with the mouth closed.

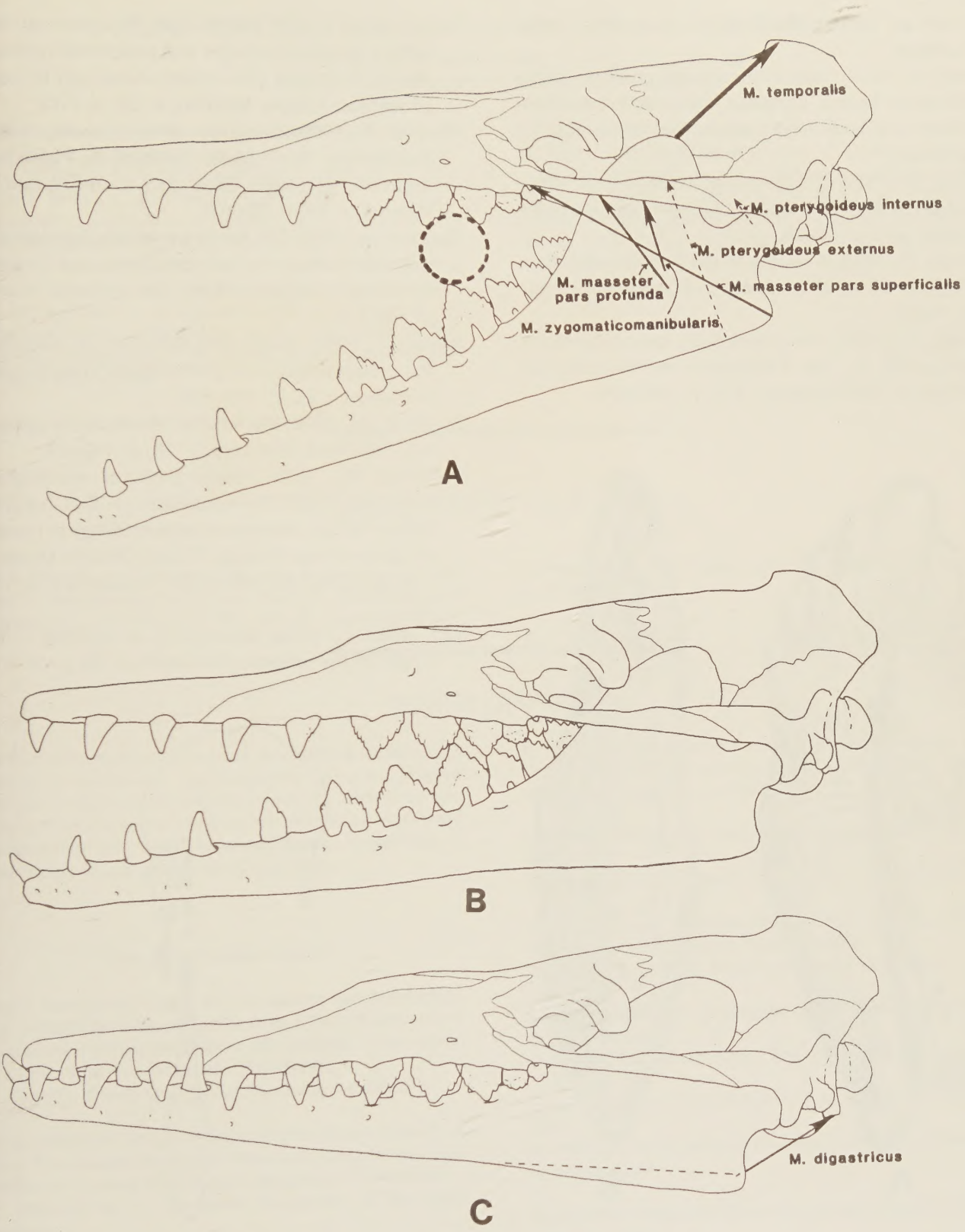

Figure 10. Bite cycle of *Zygorhiza kochii*. A, initial bite, arrows show direction of pull of muscles; dashed circle shows how prey is secured by the triangular teeth. B, cheek teeth pass by each other. C, mouth closed, bite complete, digastricus now opens mouth back to position in A.

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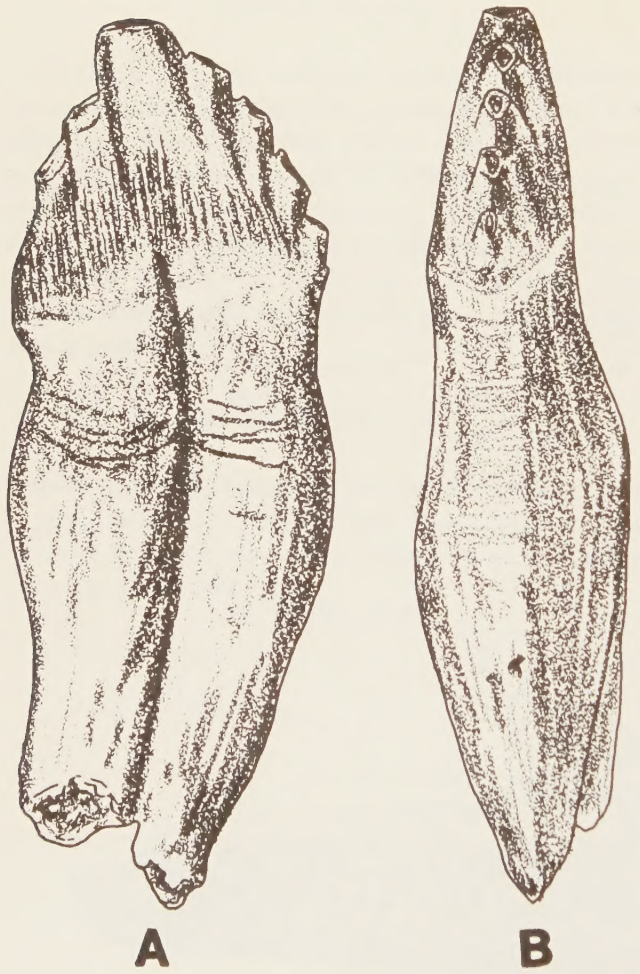

Figure 11. Isolated Archaeocete whale tooth showing wear of denticulation tips in lateral (A), and anterior (B) views. Modified from Kellogg, 1936.

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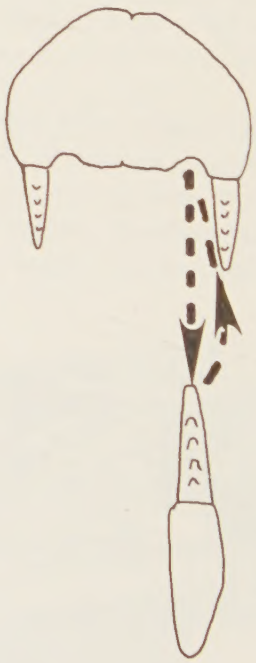

Figure 12. Cross-section through the snout of *Zygorhiza* at PM^3 showing the path of the tip of PM_3 (dashed line) during a bite cycle.

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